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Persistence of Introduced Populations of Roesel's Bush-Cricket *Metrioptera roeseli* in a Patchy Landscape

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Abstract

Introductions are likely to increase in importance as a conservation tool. Still lacking are studies directed at the distinct aspects of species introduction and their underlying assumptions. One of the most important factors determining colonization success is the propagule size. Other factors of importance for successful colonization include target area suitability. This thesis shows how different landscape and population variables affects individuals and thereby populations. Different sized propagules of Roesel's bush-cricket *Metrioptera roeseli* were experimentally introduced onto 70 habitat islands, previously uninhabited by the species, in south-eastern Sweden. The areas of introduction were carefully monitored for six years. The study showed that large propagules resulted in larger populations during the years following introduction. Propagule size had a significant effect on colonization success, i. e. large propagules were more successful in colonizing new patches. Suitable habitats were important for population persistence. Connectivity in the form of linear landscape elements and nodes were important for colonization success, population growth and dispersal. Linear landscape elements and nodes also reduced the negative effects of isolation from suitable habitat. I found that individuals avoided habitat edges and that corridors were a preferred alternative for dispersal. The corridor showed a steering effect and directed individuals to the connected habitat patch. Within six years, morphological differences in the populations could be measured. Male trait sizes were positively affected by numbers of nodes in the landscape, by the amount of linear elements, patch size, and growth rate of the population. Female trait sizes were most affected by the growth rate and the density of the population. Males showed less asymmetry in landscapes with more good habitat and connectivity, and also if they came from large initial propagules. These results stress the importance of connectivity in the landscape for population survival in both short and long term, by reducing the negative effect that habitat fragmentation has on small populations.

Key words: introduction, colonization, propagule size, linear elements, nodes, connectivity, growth rate, dispersal, asymmetry, morphological differentiation, *Metrioptera roeseli.*

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Introductions are likely to increase in importance as a conservation tool. Still lacking are studies directed at the distinct aspects of species introduction and their underlying assumptions. One of the most important factors determining colonization success is the number of individuals that constitute the propagule (the number of colonizing individuals). A population founded by a small number of individuals is more likely to represent a smaller diversity of the genetic variation than the original population resulting in a reduced resilience to environmental and demographic disturbances. Other factors of importance for successful colonization include target area suitability. This thesis shows how different landscape and population variables affects individuals and thereby populations.

Different sized propagules of Roesel's bush-cricket *Metrioptera roeseli* were experimentally introduced onto 70 habitat islands, previously uninhabited by the species, in farmland fields in south-eastern Sweden. The areas of introduction were carefully monitored for six years. The study showed that large propagules resulted in larger local populations during the years following introduction. Propagule size had a significant effect on colonization success, i. e. large propagules were more successful in colonizing new patches. Suitable habitats were important for population persistence. Connectivity in the form of linear landscape elements and nodes were important for colonization success, population growth and dispersal. Linear landscape elements and nodes also reduced the negative effects of isolation from suitable habitat. I found that individuals avoided habitat edges and that corridors were a preferred alternative for dispersal. The corridor showed a steering effect and directed individuals to the connected habitat patch. Within six years, morphological differences in the populations could be measured. Male trait sizes were positively affected by numbers of nodes in the landscape, by the amount of linear elements, patch size, and growth rate of the population. Female trait sizes were most affected by the growth rate and the density of the population. Differences between the sexes were also noted, with males being affected by more variables than females. Males showed less asymmetry in landscapes with more good habitat and connectivity, and also if they came from large initial propagules.

These results stress the importance of connectivity in the landscape for population survival in both short and long term, by reducing the negative effect that habitat fragmentation has on small populations.

Key words: introduction, colonization, propagule size, linear elements, nodes, connectivity, growth rate, dispersal, asymmetry, morphological differentiation, *Metrioptera roeseli*.

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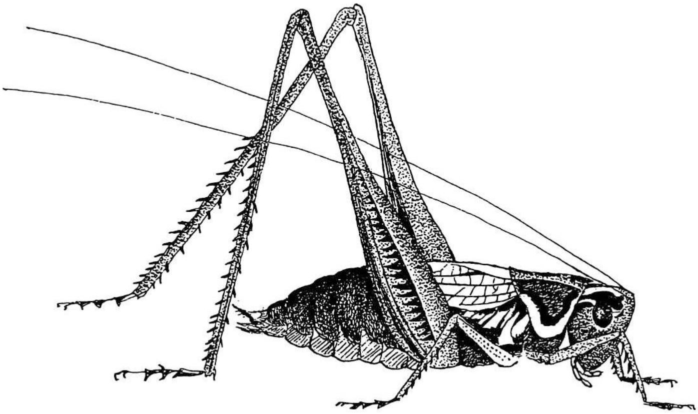

Contents

Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Berggren, Å. 2001. Colonization success in Roesel's bush-cricket *Metrioptera roeseli* the effects of propagule size: an experimental study. Ecology 82(1):274-280

II. Berggren, Å,, Carlson, A. and Kindvall, O. 2001. The effect of landscape composition on colonization success, growth rate and dispersal in introduced bush-crickets *Metrioptera roeseli*. Journal of Animal Ecology 70(4):663-670

III. Berggren, Å,, Birath, B. and Kindvall, O. 2001. Effect of corridors and habitat edges on dispersal behavior, movement rates and movement angles in Roesel's bush-cricket *Metrioptera roeseli*. Submitted manuscript.

IV. Berggren, Å. The effect of propagule size, landscape structure, growth rate and dispersal on morphological differentiation and asymmetry in introduced bush-crickets *Metrioptera roeseli*. Submitted manuscript.

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Introduction

Introduction of species

Species introduction has a lengthy history, possibly as long as there have been humans on earth. The reasons for introductions have been numerous. Species have been introduced as game, for biological control (sometimes to reduce negative effects of earlier introduced species), for aesthetical purposes, or unintentionally as stowaways (Mayr 1964, Roots 1976, Armstrong 1982, den Hartog & van der Velde 1987, Le Hénaff & Crête 1989). However most introductions fail (Berry, et al. 1982, den Hartog & van der Velde 1987) often due to non-optimal design or being performed in a way unsuitable for successful colonization (Oats & Warren 1990).

Reasons for undertaking species introductions have changed in recent times. From being a way to increase the suitability of an area for humans, introductions today are mostly directed towards improving the survival chances of the introduced species by expanding its range (Roots 1976, Atkinson 1989, Stanley Price 1989, Bright & Morris 1994, Stussy, et al. 1994, Nevé, et al. 1996, Marshall & Edward-Jones 1998). The method is employed in many conservation programs (Griffith, et al. 1989, Short, et al. 1992, Toone & Wallace 1994, Sherley 1995, Sjöåsen 1996, Fritts, et al. 1997, Combreau & Smith 1998) and is likely to increase in importance as a conservation tool as habitat destruction and fragmentation increases. To enhance the success of conservation work, special programs and comities have been formulated to gather knowledge and develop protocols. Still lacking in this area of conservation research are studies directed at the distinct aspects of species introduction and their underlying assumptions (Caughley 1994). Why this research has not progressed as rapidly as the actual introductions is best explained by examining the nature of the problem itself. When working with threatened species there is often an air of urgency around the work, and it is commonly thought that time should be used to take action immediately rather than doing "time wasting" pre-introduction research. Another concern is that because of the threatened status of the species in question, it may appear risky to conservation managers to involve valuable individuals in studies involving handling or moving and thus such studies are often avoided. This attitude may compound problems in the longer term as present and future introductions may fail or succeed without it being clear as to why they did so. This may sacrifice more individual animals and delay successful introductions significantly more than the pre-introduction research would have done, without the benefit of understanding why it succeeded or failed. A good intention to save individuals from disturbance may instead reduce the viability of these populations.

An alternative approach to studying individuals from the threatened population is to use a model species. Ideally the model species should be similar enough to the species in question in morphological characteristics, behavior or habitat use, so that meaningful results can be obtained from studies undertaken on them. The model species' conservation status should be lower than species the results will be used for, allowing greater manipulation of introduction variables than would otherwise be possible. The obvious concern in using this procedure is that there are always differences between species, so caution in generalizing results to other species must always be kept in mind.

Factors affecting introduced populations

One of the most important factors determining colonization success is the number of individuals that constitute the propagule (the number of colonizing individuals); with the larger the propagule, the higher the chance of success (Crowell 1973, Veltman, et al. 1996, Green 1997). There is probably a critical propagule size that greatly enhances colonization success (Richter-Dyn & Goel 1972) and this differs between species. One impediment to successful colonization is random extinction before a viable population has been established. The highest risk of extinction is associated with small populations (Richter-Dyn & Goel 1972). Populations are usually founded by very small propagules, and in the initial stages of colonization these populations therefore experience a high risk of extinction due to demographic or environmental stochasticity (Ebenhard 1991).

Other factors of importance for successful colonization include target area suitability, e. g. high vegetation quality and amount (Levins & Heatwole 1973, Berry et al. 1982, Griffith et al. 1989, Oats & Warren 1990), and community features (Pimm 1991). Habitat loss and fragmentation are considered to be major threats to species today (Fahrig 1997). Habitat loss can affect populations in many ways, most obviously by reducing the space of suitable habitat for populations. Fragmentation means loss of connectivity (i.e. the functional linkage among habitat patches) (Lord & Norton 1990), which reduces the opportunities for individuals to successfully move between habitat patches (Klein 1989, Baguette, et al. 2000). This is important because dispersal can aid in maintaining small populations and extend species ranges. This is done by immigration supplementing local populations and decreasing the risk of demographic stochasticity and inbreeding depression by increasing gene flow (den Boer 1990, Cunningham & Moritz 1998). Knowledge of how both habitat loss and habitat fragmentation in landscapes affect introduced species is important in understanding the impact of these variables (Hanski & Thomas 1994, Thomas & Hanski 1997). Connectivity in an anthropogenic landscape often occurs as linear elements (corridors). These elements can facilitate dispersal in both mammals and insects (Henderson, et al. 1985, Munguira & Thomas 1992, Mauritzen, et al. 1999, Niemelä & Spence 1999). Linear landscape elements are assumed to limit the negative effects of habitat fragmentation by increasing landscape connectivity (Dunning, et al. 1992). Evidence from some studies suggests that they are valuable as conservation tools, and that they increase population persistence for species that view the matrix as hostile (Beier & Noss 1998). Linear landscape elements are also connected to each other in intersection areas, so-called nodes (Forman & Godron 1986). A proposed method for moderating the negative effects of habitat isolation is the preservation or restoration of linear landscape elements that structurally link otherwise isolated habitat remnants (Saunders & Hobbs 1991). These corridors are meant to increase landscape connectivity by facilitating movement of organisms between habitat fragments and thus minimizing the risk of inbreeding and extinction.

If a population is founded by a small number of individuals it is more likely that they will represent a smaller diversity of the genetic variation in the original population resulting in a founder effect (Mayr 1954). The new population will have lower genetic variability possibly reducing its resilience to environmental and demographic disturbances. The individual's inability to cope with the environment during development can be seen in effects on trait size and asymmetry. It has been demonstrated in several studies that populations that suffer from genetic loss and environmental stress show an increase in asymmetry (Parsons 1990, Møller 1993).

The results in this thesis present new information of which variables can affect populations, whether they are introduced or not. The difference between already existing populations and introduced populations may sometimes be very small. Both can consist of a small number of individuals with a restricted genetic diversity resulting from random dispersal through the landscape or a limited population number for other reasons. This makes it likely that landscape and population variables affect populations (whether they are introduced or 'natural') in similar ways. Therefore the conclusions made from these studies can also be used to understand how already existing populations function and react.

The aim of this thesis is to study how different landscape and population variables affect individuals and thereby populations. All the studies are experimental and the species used in these studies is Roesel's bush-cricket *Metrioptera roeseli.* Three of the four papers in the thesis (I, II and IV) are studies conducted on large-scale introductions of the species. In *Paper I*, I examine how colonization success is affected by differences in propagule size. The effect of landscape composition on colonization success, growth rate and dispersal is examined in *Paper II. Paper IV* demonstrates the effect of propagule size, landscape structure, growth rate and dispersal on morphology and asymmetry in the introduced populations. *Paper III* is a micro-scale experiment focusing on the effect of specific landscape variables on movement of individuals.

Methods

The species

Roesel's bush-cricket is a small species, 12-18 mm in length (Dunning et al. 1992) and is common in south and central Europe, Finland and Latvia. In Sweden the species is predominantly found in the south-east around Lake Mälaren. Their preferred habitat is moist ungrazed tall-grass areas where they feed on grass, grass seeds and small insects. Nymphs often feed on flower parts and pollen (Marshall & Haes 1988). Eggs are laid during summer and autumn in grass stems and these hatch in May one or two years later (Ingrisch 1986). The nymphs progress through 6 instar phases before becoming adults (Marshall & Haes 1988). Adult males stridulate from July to October and if the weather is warm or sunny they will stridulate almost continuously at this time during the day. The song is characteristic, making the males of this species easy to census. A variable proportion of the population are macropterous (winged), but these number less than 1% (Vickery 1965).

The large scale experiment

M. roeseli is not a threatened species and is currently expanding its distribution in Sweden (Pettersson 1996). Because of this it is an ideal model species as there is no impediment to using it from a conservation perspective. Its current restriction to well-defined areas in the south-east of Sweden and its documented range expansion make it an excellent candidate for introduction experiments. Moving it from areas where it occurs abundantly to areas where it has yet to colonize means that individuals later found in the introduction sites were either the originally introduced individuals (if found the same year) or their descendants. This ensured that there would be no confusion with already existing individuals and allowed easy interpretation of the species ability to establish and expand in the landscape. The south-western introduction sites were the closest to the current natural species distribution and it was estimated that they would naturally colonize these areas within 5-10 years.

The introductions

Different sized propagules of *M. roeseli* were introduced onto 70 habitat islands, previously uninhabited by the species in a large-scale experiment in 1994-1995 (Fig. 1, 2). These consisted of five different sizes (number of individuals) with an even sex ratio. The smallest propagule contained only 2 individuals (one male and one female), with the other sizes numbering 4, 8, 16 and 32 individuals. All introduced bush-crickets were in the last nymphal stage and hence virginal. The experimental areas were situated in the agricultural landscapes in the counties of Uppland and Stockholm, located in south-eastern Sweden. The habitat islands consisted of

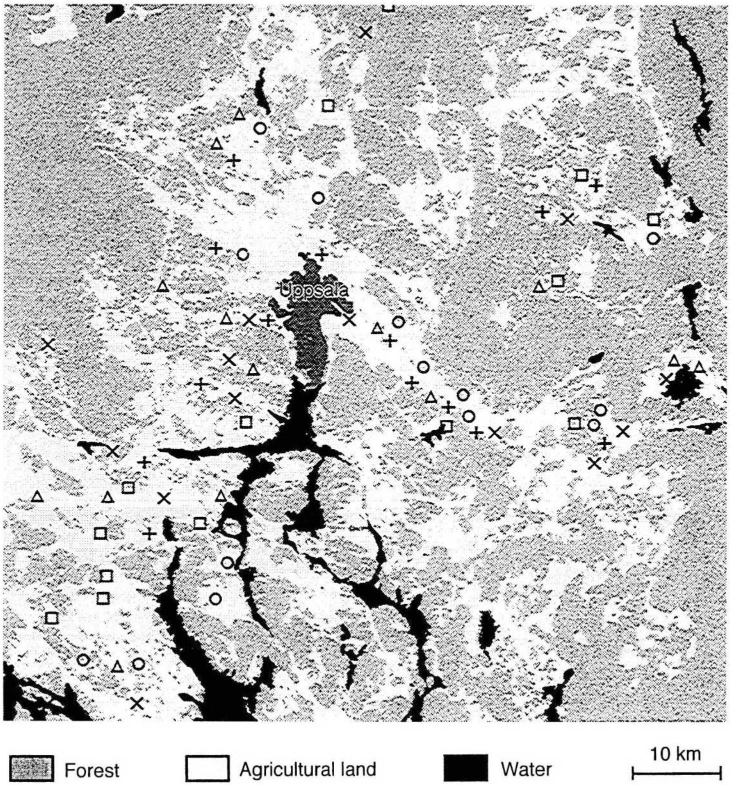

Figure 1. Map over introduction sites in the agricultural landscape around Uppsala town. += propagule size 2, ○=propagule size 4, Δ=propagule size 8, ×=propagule size 16, □=propagule size 32. The current distribution of the species is outside the map.

patches of ungrazed semi-natural grasslands of varying sizes (264 m^2 - 8642 m^2) within arable fields. Due to the common rotation system used by the farmers, the use of fields changed every season and included cereal crops, fallows and leys. Some of the selected habitat islands were connected to other suitable habitat patches (unoccupied by *M. roeseli*), while others were isolated by up to 85 m. The minimum distance between introductions was 2 km. The surrounding matrix consisted of arable fields, forests and human settlements including potential barriers such as creeks and roads (de Jong & Kindvall 1991, Kindvall & Ahlén 1992). Although the type of landscape was the same for all introductions, the sites differed in the amount and number of different landscape variables. The minimum distance from the edge of the current distribution of *M. roeseli* was 17 km. The propagules were then randomly distributed across these patches. There were no differences between the five propagule sizes regarding the landscape composition or structure they were released into (Pearson product-moment correlation, $r<0.5$).

Population censuses

A minimum area of 30 ha around the introduction patch was censused annually from the year of introduction at the end of the reproductive season (i.e. August and September). Within this area more than 95% of the males present are expected to be detected (de Jong & Kindvall 1991). With the dispersal of individuals, the censused area increased after the first year up to 78 ha around the introduction patch. Censuses were undertaken by listening for stridulating males. An ultrasound detector (Pettersson D 960) was also used to detect individuals more effectively at longer distances. Roads were also used as census locations at a distance of approximately 2 km from the release point when entering and leaving the sites. The inventories were made only in warm (ca >18° C), dry and sunny weather between 9 a.m. and 4 p.m to maximize detection. Numbers of males found at each site and their locations were entered on digitized maps. Presence of one or more stridulating individuals was the criterion for successful colonization. As a measure of population increase or decrease, in *Paper II* I use the ratio of the number of individuals introduced and number of individuals recorded in 1999. In *Paper IV* the equation $N_t = N_0 e^{rt}$ is used to get an r-value for the population. N_t for the populations was taken as the number of individuals recorded in 1999. The different measurements of r were correlated (Spearman rank correlation, $r=0.7$, $p=0.048$). Dispersal distances from the center of the habitat patches were measured for each individual to the nearest 1.0 m. A population mean was then calculated from this data in *Paper II*. In *Paper IV* distance between individuals was measured for each individual to all other individuals to the nearest 1.0 m. A population mean on dispersal was then calculated from this data.

Habitat mapping

Maps (1.5 x 1.5 km) centered around the introduction patch of all introduction sites were digitized and used for *Paper II* and *Paper IV* (in *Paper I* the two landscape variables were measured by hand from maps). Five different types of landscape elements were defined based on information found on land use maps (scale 1:10 000) and habitat mapping during field-visits. These include arable fields, forests, semi-natural grasslands, uninhabitable land (housing areas, streams, lakes), and linear landscape elements (ditches, road verges). Areas of all landscape elements were measured on the digitized maps. Data on patch size, their isolation from other suitable habitats and the number of nodes (intersections of linear landscape elements) were also estimated from the maps (see Table 1). A number of these landscape variables were correlated. Arable field area and forest area were negatively correlated (Pearson product-moment correlation, r=-0.78, p<0.0001), arable field area and degree of isolation were negatively correlated (Pearson product-moment correlation, r=-0.51, p<0.0001), and the number of nodes was positively correlated with the amount of linear landscape elements (Pearson product-moment correlation, r=0.69, p<0.0001). The other correlations between landscape variables were only weakly correlated (all r <0.5). Due to the correlation with both area of forest and degree of isolation from suitable habitat, the variable areas of the arable fields were excluded from the analyses in *Paper II*. This is because there is largely an either/or presence of arable field or forest, and forests seem to show biologically interesting features for the bush-cricket. In *Paper IV* a reduced set of variables was used; patch size, linear elements and nodes. Although nodes and linear elements show a positive correlation it was decided to keep both variables in the analyses due to their evident importance and effects on population survival and distribution. In the analyses, landscape data within a radius of 238 m from the center

Table 1. Descriptive statistics for independent variables used in analyses of habitat features affecting Roesel's bush-cricket population dynamics

Variables	minimum	mean	maximum	SE
Field (ha)	4.32	10.8	15.4	0.35
Forest (ha)	0	3.01	11.2	0.34
Grassland (ha)	0.85	3.10	9.87	0.20
Isolation (m)	0	20.3	84.9	2.18
Linear landscape element (ha)	0.50	1.32	2.06	0.05
Nodes (no)	0	3.09	7	0.23
Patch size (ha)	0.02	0.17	0.86	0.02
Uninhabitable land (ha)	0	0.09	2.26	0.04

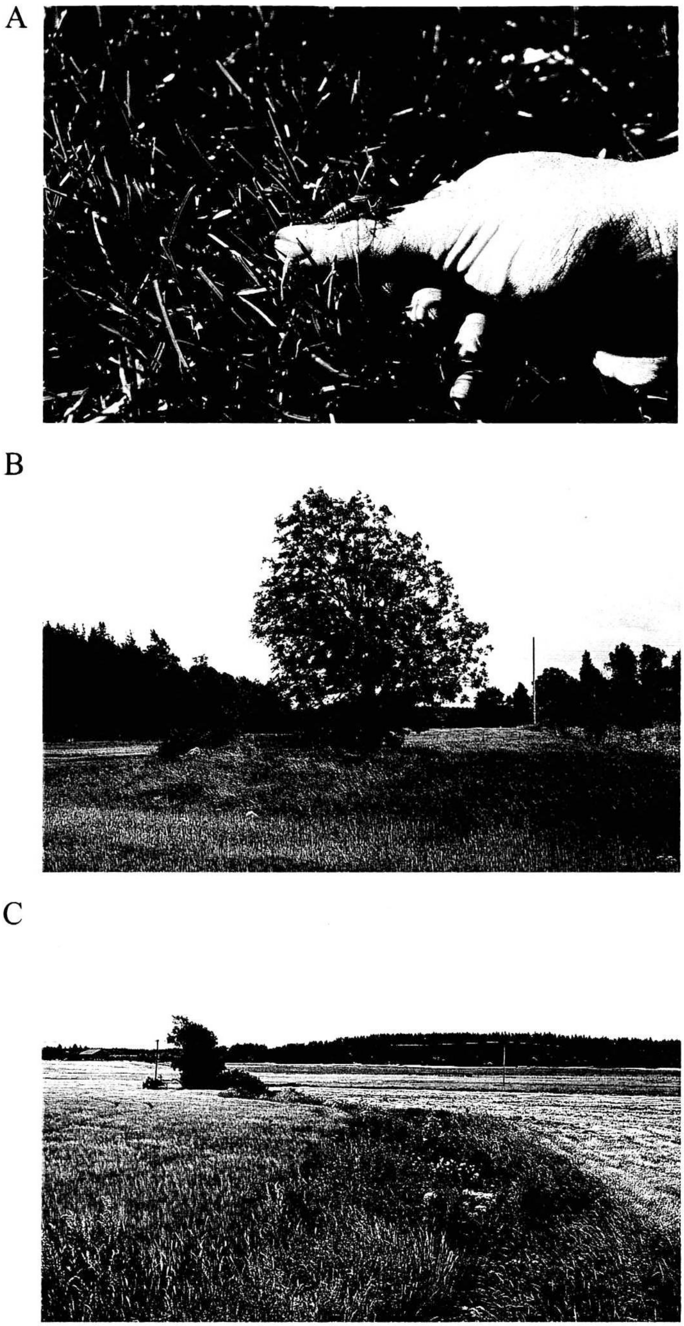

Figure 2. a) a male *Metrioptera roeseli*, b) one of the introduction patches (suitable habitat in a crop field), c) a landscape variable that was tested in the studies - a linear landscape element (in this case a ditch between fields).

of the habitat island was used. The choice of 238 m is based on the 95% limit of dispersal data from all individuals in the first year after introduction. This distance was used to get a suitable estimation of the landscape that might be encountered by individuals (and affecting them). Because of a change in use of the field surrounding the introduction patch from initially cereal crops to ley or fallow in some localities, the landscape data from the first year will represent all years.

Studying morphological differentiation and asymmetry

Six years after the bush-crickets were introduced, a sample of individuals was caught. This was done to study the effect of both landscape and population variables on morphology and asymmetry in the individuals (*Paper IV*). Nine populations from the different propagules that resulted in successful colonizations were chosen. From all propagule sizes, two populations were sampled, with the exception of the smallest propagule size. Only one population was sampled from the smallest category (initial propagule size two individuals) because only one viable population still existed. This resulted in 192 animals divided between the different propagule sizes as follows; 20 individuals from propagule size 2, 51 individuals from propagule size 4, 41 individuals from propagule size 8, 40 individuals from propagule size 16 and 40 individuals from propagule size 32. For comparison, 25 individuals from the original collecting site for the introductions were also caught. This resulted in total 217 animals used in the study.

Individuals were caught by hand netting during August 2000. They were then killed by freezing. After 24 hours they were weighed with a Sartorious scale, then put in alcohol and measured within 2 days of being caught. A micro enhancer (x 10) with built-in ruler was used to determine the different body measurements. In addition to the individuals' body weight and body length, three different traits were measured. Maxillary palp length was measured as the length from the maxillary/maxillary palp joint to the end of the maxillary palp, fore wing length was measured from the wing joint to the end of the radial sector, while hind tibia length was measured from the femur/tibia joint to the tibia/tarsus joint. The fluctuating asymmetry (FA) is the absolute value of this measure. An estimate of measurement error was required in testing for the presence of FA and this was done to determine if between-sides variation was significantly larger than measurement error in a mixed model two-way ANOVA performed on repeated measures. This analysis was undertaken on 10 individuals measured "blindly" twice and showed that FA was significant relative to measurement error in all three traits, maxillary palps ($MS=1.53$, $p<0.05$), tibias ($MS=0.80$, $p<0.0001$) and wings ($MS=32.81$, $p<0.0001$). Morphological and asymmetry analyses were done separately for the sexes. This was done due to the potential for unknown influences that could affect the sexes differently.

The small scale experiment

Linear elements appeared important for individual dispersal through the landscape in *Paper II*. To examine this further a smaller scale experiment was undertaken (*Paper III*). This experimental study was carried out between the 28th of July and the 15th of September in 1997 and 1999 at two different locations (59° 44'N 17° 48'E and 59° 49'N 17° 38'E) in the county of Uppland, south-eastern Sweden. Only adult male bush-crickets were used because their call behavior makes them easy to monitor and it prevented a reproducing population being introduced into the study site. The experiments were only made in relatively warm (ca >15° C), dry and sunny weather between 9.35 a.m. and 4.40 p.m. as this is when the bush-crickets are most active.

The experimental areas consisted of ungrazed semi-natural grasslands, with vegetation dominated by tall timotheii grass (*Phleum pratense*) and clover (*Trifolium sp.*). Test areas were created within the study site consisting of a matrix of low cut grass (approximately 5 cm high) where a central area and a corridor extending out from this was left uncut (approximately 60 cm high) (see Fig. 3). Corridor direction in the test areas varied (north, east, south and west) to avoid confounding effects of movement behavior associated with corridor direction. The areas had a radius of 575 cm of which the central circle had a 75 cm radius, giving the corridor a length of 500 cm. Two different sets of test areas were cut. The first with a "hard edge", where a sharp border between cut an uncut grass existed. The other with a "soft edge", where a buffer zone of half cut grass (approximately 30 cm high) of half the corridor width was left around the center and along the entire corridor. All preparations of the test areas were carried out before any individuals were released. For hard edged test areas, the corridor width was 47 cm (10% of the central circle's circumference) and for test areas with a soft edge the corridor's width was doubled to 94 cm (15% of the central circles circumference) (Fig. 3). The corridor sizes and shape are similar to agricultural linear landscape elements such as field edges and road verges.

Individuals were released one at a time per experimental trial in the middle of the test area's central patch. The area was then censused by listening for the stridulating male every ten minutes and all positions of the individual were recorded. For every individual, dispersal distance and the direction from the center of the habitat patch were measured. The experiment was stopped when the individual reached the uncut grass outside the test area or if an individual stayed in the central patch for a longer time than two hours. If it did not move in this time it was regarded as stationary and removed. An individual not heard after release during the experiment was regarded as having been preyed upon. If an individual was found

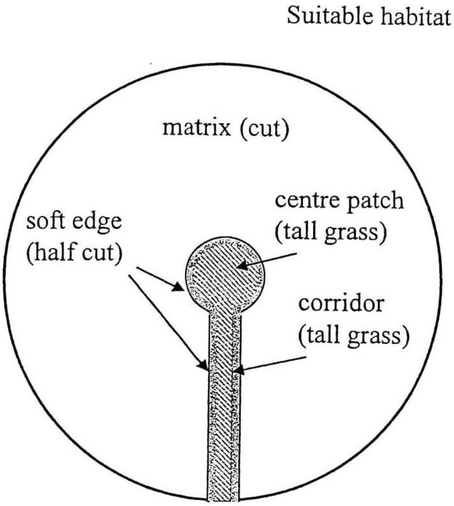

Figure 3. Test area showing the central patch connected to external suitable habitat with a corridor. The central patch and corridor consisted of tall grass habitat, and the matrix was cut grass. For test areas with soft edges, an additional grass strip with half the grass height was left untouched around the center habitat patch in the corridor.

outside the test area and within ± a 30° arc of the corridor entrance, it was presumed to have moved through the corridor despite no records of the individual's movement being noted. Direct observations of individuals silently moving through the matrix or corridor help validate this assumption.

From an individual's measured positions during the experiment, calculations of dispersal behavior, moving angles and step lengths (distance between two following positions) and thereby dispersal rate could be determined. Two types of moving angles were investigated which were called turning angles and center angles. The turning angle was calculated from the angle between three successive positions. The center angle was determined from the angle between the center (release point), and two following positions in the central habitat. Whether the angles were towards the left or right was not considered.

Results and discussion

Size does matter - How propagule size influences colonization success

One of the most important features determining whether or not a species will successfully colonize an area is the size of the introduced propagule. In *Paper I*, I examined the colonization success in the 70 introduced populations to see what effect the propagule sizes had on the probability of colonization. I found that patches with large initial propagules had larger local population sizes for all periods after introduction as more individuals were found in all census periods (χ^2=27.2, df=12, p=0.0073). The probability for successful colonization of an area increased with increasing propagule size (Fig. 4). Three months after introduction (at the end of their first breeding season), survival of local populations increased with propagule size from 21.4 to 75.6% (χ^2=13.5, df=4, p=0.0066). One year after the experimental introduction a similar pattern was found. Survival of local populations increased with propagule size from 7 to 64% (χ^2=17.2, df=4, p=0.0008). Two years after the experimental introduction, all local populations founded by a propagule size of two

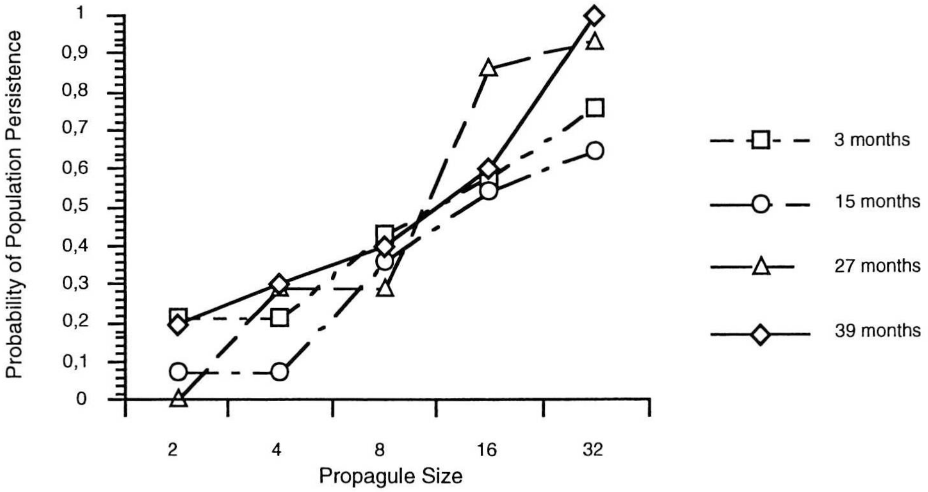

Figure 4. Persistence of local populations for three years after introduction of variable propagule sizes.

individuals had become extinct, while survivorship of the remaining local populations ranged from 30 to 93% (χ^2=36.5, df=4, p<0.0001).Three years after the experiment was initiated the pattern was the same for the reduced dataset of 50 introductions. Propagules that initially were smaller showed a higher extinction risk. For a propagule size of two individuals, 20% now persisted, showing that the absence of individuals in some areas the year before was a pseudoextinction. Persistence in the remaining local populations of larger propagule sizes ranged from 30 to 100% (χ^2=16.0, df=4, p=0.003).

The pseudoextinctions that occurred in some localities can be explained by the special life cycle of *M. roeseli.* Depending on various environmental cues, e.g. photoperiod, experienced by the female at the time of oviposition, eggs become programmed to hatch either the following spring of the spring one year later (Ingrisch 1984). Increase in colonization success in some patches due to immigration of individuals from other patches (naturally occurring or introduced) is highly unlikely. As mentioned earlier, the species does not naturally occur in these areas and consequently all populations found in the study area arose from my introductions. The longest distance recorded for individual movement from an introduction site is about 300 m in 3 years. This distance is less than 1/5 of the nearest distance between two introduction patches, arguing against movement between these patches during my study.

An Allee effect (Allee 1938) due to reduced mating opportunities can occur when propagules are small. But, in an experimental study by (Kindvall, et al. 1998), no Allee effect was detected in *M. roeseli* in densities as low as 1% of normal. The animals effectively found mates even at low densities, simply by adjusting their movement behavior. The results from my study show that as few as four individuals can establish a persistent local population, but the success rate is much lower than with the larger propagules. If future introductions were to be made with this species or a similar species, a propagule size of at least 32 individuals would be required to establish a viable population with a high probability of persistence. However, this number should be used judiciously when the goal is conservation, since the introduced *M. roeseli* have in this study only been followed for three seasons since introduction.

The missing link - Effects of landscape composition on population variables

Habitat suitability is likely to be very important for establishing an introduced population. An ideal habitat would be suitably large, heterogenous and would allow opportunities for movement between patches when conditions fluctuate. In *Paper II*

I studied the effect of the landscape on population parameters in the experimentally introduced populations. Populations in landscapes with many linear landscape elements showed a higher colonization success than populations with fewer (Table 2, Wald χ^2=6.45, df=1, P=0.011). This was the only landscape variable that had an effect on colonization success.

Population growth rates declined with increasing isolation from suitable habitat and more forest in the landscape (Table 2). However, population growth rates increased with the area of grassland, the number of linear landscape elements, the number of nodes and patch size (Table 2). Interaction effects were significant between area forest and grassland and patch size (Table 2), with higher population growth in landscapes with larger areas of grassland and larger patch sizes, but with less forest. There were also significant interactions between isolation from suitable habitat and linear landscape elements and nodes (Table 2), with lower population growth in more isolated patches in landscapes with few linear landscape elements and nodes.

Table 2. Summary of the forward, stepwise, linear multiple regression models identifying predictors of population growth and dispersal distance. Terms with more than one component, separated by • indicate interactions between component terms

	Population growth				Dispersal distance			
Variable	Est.	F-ratio	d.f.	P	Est.	F-ratio	d.f.	P
Forest	0.22	3.14	3	0.032	0.68	5.01	2	0.011
Grassland	2.77	3.40	2	0.040				
Isolation	-1.52	3.35	3	0.025				
Linear landscape element	-0.48×10^{-3}	2.62	2	0.082				
Nodes	1.39	5.44	2	0.007	53.8	8.02	2	0.001
Patch size	2.31	3.70	2	0.031				
Interactions:								
Forest • Grassland	-14.4×10^{-3}	5.42	1	0.023				
Forest • Nodes					-0.24	9.97	1	0.003
Forest • Patch size	-10.6×10^{-3}	4.12	1	0.047				
Isolation • Linear landscape element	0.18×10^{-3}	5.23	1	0.026				
Isolation • Nodes	-0.387	6.87	1	0.011				
	n=70, R^2 adj=0.237				n=50, R^2 adj=0.211			

Dispersal distance was higher in all years for individuals from populations with higher population growth (F=8.30, df=1, p=0.005). There was a significant negative effect of the area of forest on dispersal distance and a significant positive effect of nodes on dispersal distance (Table 2). There was also a significant effect of the interaction between the number of nodes and the area of forest on dispersal distance (Table 2), with longer dispersal distances in landscapes with many nodes and smaller areas of forest.

The effect of landscape structure on colonization success is not well understood. For *M. roeseli*, linear landscape elements, i.e. ditches and road verges, seem to be important. It is thought that linear elements facilitate dispersal in this insect as it walks from patch to patch, and that this connectivity increases access to a greater spectrum of habitats. The structure of linear elements also results in sharp gradients (both vertically and longitudinally) of biotic and abiotic conditions. These environmental factors can change within and between seasons, and habitat heterogeneity can reduce the risk of population extinction (Dunning et al. 1992, Kindvall 1996). As *M. roeseli* lays its eggs in grass stems in relatively moist areas, a gradient of humidity in the linear elements and a good opportunity to disperse to moist areas may be fundamental for the development of the eggs. The value of linear landscape elements, both for dispersal and reproduction, has also been shown in other studies (de Maynader & Hunter Jr 1999, Laurance & Laurence 1999).

Large areas of forest had a negative effect on population growth, with higher growth rate in landscapes with smaller forest areas. Apart from the fact that the forest itself is an unsuitable habitat (de Jong & Kindvall 1991), the vegetation in road verges and in ditches in the forests also differs from the vegetation in road verges and ditches in farmland areas, where grasses are more productive and diverse. The trees also cast shadows on the surrounding ground during parts of the day which lowers the temperature, possibly to suboptimal levels for the bush-cricket. A negative effect of forest on species diversity in Orthopterans has previously been noted (Samways & Moore 1991). The area of grassland had a positive effect on population increase, with a higher growth rate where there were larger grassland areas. This confirms grassland as being a good habitat for the species and shows the importance of large grasslands for population increase and thereby population viability.

Isolation had a negative effect on population growth rate, with larger growth rates in populations occurring where they were initially less isolated from good habitat. This isolation effect may be a result of decreased possibilities for individuals to reach good habitats and colonize them (Hjermann & Ims 1996, Haddad 1999), which is crucial if the vegetation on the introduction patch deteriorates. The isolation may also have depleted the original patch of individuals by emigration and thereby decreased the possibility of survival on the patch, if emigrants did not return from unsuccessful explorations through the matrix (Sih, et al. 2000).

There was a higher growth rate in the populations in landscapes with more linear landscape elements than in those with fewer. The linear elements offer both suitable habitat for the populations to grow in and also offer, as discussed earlier, an opportunity to move through the landscape and find suitable habitat when there are changes in weather and vegetation.

Populations in landscapes with many nodes had a higher population increase than populations in landscapes with fewer. Although the nodes are slightly broader than the linear elements, it is not likely that it is just this fact that increases the growth rate. The nodes probably slow the dispersal rate of the individuals (Henderson et al. 1985, Munguira & Thomas 1992, Mauritzen et al. 1999, Niemelä & Spence 1999). This makes the individuals aggregate in the nodes, a mechanism that may increase chances of successful reproduction. Such a decrease in dispersal rate has been recorded in a forest beetle *Pterostichus melanarius*, which first expands into rural areas along road verges and then more slowly colonizes adjacent deciduous forest (Niemelä & Spence 1999). The nodes also give individuals an opportunity to move further into the landscape and into new linear landscape elements with a higher chance of finding suitable habitats. This enables individuals to move in new directions and cover new areas and reach more locations further away, which increases the chances of finding patches of suitable habitat and linear elements to colonize.

It is interesting to note that population growth in *M. roeseli* is greater in larger patches. This pattern is expected as a consequence of patch-size-dependent emigration rates (Thomas & Hanski 1997). Several empirical studies have shown that the emigration rate is negatively correlated with patch size (Kareiva 1985, Hill, et al. 1996, Kuussaari, et al. 1996). The large patches not only offer areas of expansion, but probably more importantly, a greater probability of heterogeneity in vegetation that offers suitable areas for feeding and reproduction (Rosenberg, et al. 1997). It is also possible that the number of returning immigrants was higher for larger patch areas, and supported the population (Hill et al. 1996, Kuussaari et al. 1996).

There was a significant effect of interactions between isolation from suitable habitat and nodes and linear elements on population increase. The interactions had a higher degree of explanation than the separate variables. The negative effect of isolation was accentuated in populations that lived in landscapes that also contained fewer nodes and linear elements. This isolation means that it took longer for individuals to reach and colonize surrounding grassland areas and linear landscape elements (Haddad 1999). This is further emphasized if there are limited good habitat areas to find and few directions to move in. The negative effect of isolation on population growth can therefore be reduced if the landscape has many linear elements and nodes. The negative effect of forest was greater in populations in areas with smaller areas of grassland and smaller patch sizes. This interaction also had a higher degree of explanation than the separate variables, with this most likely being an effect of available habitat. Landscapes with large areas of forest and small patch sizes and small grassland areas provide few good habitats for the populations to expand in, and the available habitat will govern the level of population size.

Populations with higher growth rates dispersed further. This suggests that dispersal occurred in suitable and productive habitat (i.e. not due to unsuitable habitat). The increasing populations need larger habitats and this is shown by an expansion of the populations' distribution range. Longer dispersal distances are a result of successful colonization by the species, especially if the growth rate of the populations is high. There was a significant negative effect of area of forest on dispersal distance. Apart from being an unsuitable habitat for the species, this results in low connectivity and little availability for movement through the landscape. This has been noted in another study (Roland, et al. 2000). The number of nodes had a significant positive effect on mean dispersal distance from the introduction patch. The nodes give the landscape a two-dimensional grid system (Forman & Godron 1986), enabling individuals to move in new directions, cover new areas and reach more locations further away. This greatly increases the chance of finding patches of suitable habitat and new linear elements to colonize. This effect of enhanced dispersal in linear elements through matrix has been seen in earlier studies of many other different species, such as birds (Desrochers & Hannon 1997, Brooker, et al. 1999), insects (Munguira & Thomas 1992, Haddad 1999), amphibians (Rosenberg, et al. 1998), and mammals (Henderson et al. 1985).

In landscapes with more nodes and less forest, the dispersal distance was longer. This interaction had a higher degree of explanation than the variables alone, which shows that large areas of forest combined with few nodes have a strong negative effect on dispersal in the populations. The negative effect of unsuitable habitat (forest) (de Jong & Kindvall 1991) can therefore be reduced if connectivity of the landscape is increased.

Corridors help in finding "the greener grass on the other side"

There has been lengthy debate on whether corridors are effective dispersal agents for animals. In *Paper II* I found that for introduced populations linear elements (corridors) had a significant effect on several population parameters. To study the extent corridors were used in dispersal and how this affected individual movement, I conducted a total of 131 experiments, each monitoring the dispersal behavior of an individual bush-cricket (*Paper III*). Of these, nine individuals were lost, probably due to predation and were not included in the analyses. Of the remaining 122 individuals, 60% (73 individuals) moved out from the central patch and of these

44% (32 individuals) moved out of the test area through the corridor. This use of the corridor during dispersal was highly significant (χ^2=17.94, p<0.0001) (Fig. 5). This preference to use corridors was significant for both hard edged (χ^2=9.93, p<0.001) and soft edged (χ^2=8.32, p<0.05) habitats. All individuals that entered the corridor from the central patch continued moving through the corridor until entering the surrounding habitat. This ability of the corridor to influence the dispersal direction of bush-crickets is significant as only 16% (5 individuals) would be expected to move along the entire length of the corridor if their movement were random (χ^2=46.7, p<0.0001). The edge type (hard or soft) did not influence whether individuals moved through corridors or matrix (χ^2=0.17, p=0.68). Furthermore, there was no difference between individuals that moved over matrix or through corridors in how long they waited before they exited from the central habitat (t=1.59, p=0.12).

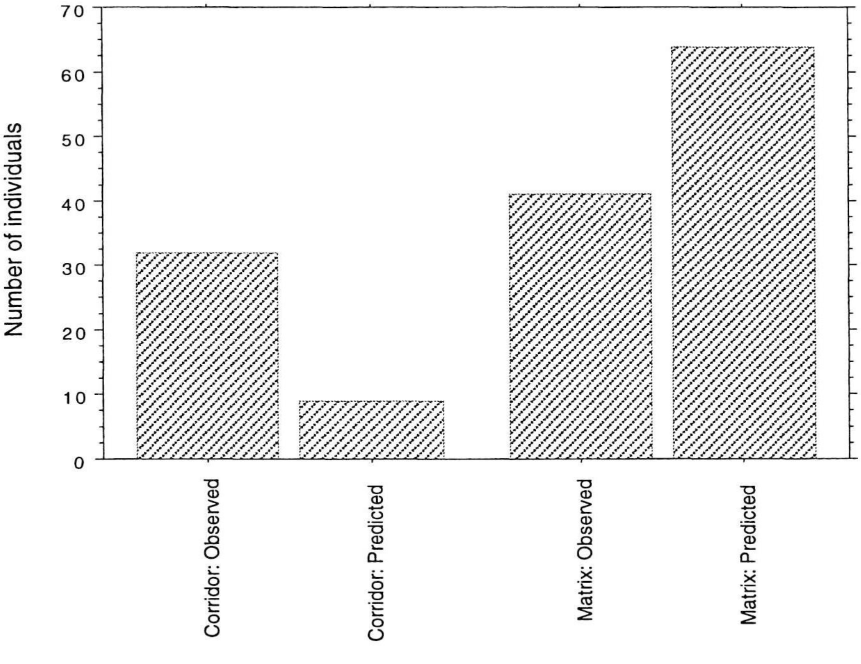

Figure 5. Numbers of individuals using the corridor to move from the central patch to suitable habitat outside the test area are significantly greater than is predicted if their dispersal were random.

The turning angles differed in corridors and matrix. Turning angles in the corridors (149.5° ± 8.8, n=14) were significantly larger than in matrix (96.5° ± 13.13, n=19), i.e. individuals moved more linearly in corridors than in matrix ($t=3.10$, $p=0.01$). In addition, individuals moved faster (distance/unit time) in matrix than through corridors ($t=2.37$, $p<0.05$). Individuals in the central patch moved slower in comparison to those in corridors ($t=12.4$, $p<0.0001$) and matrix ($t=14.1$, $p<0.0001$). The center angles were correlated with the distance from the center. The angles were smaller near the edge of the central patch when compared to those nearer the center (Spearman rank correlation $r=0.22$, $p<0.05$). There was no correlation between step length and distance to edge. Edge hardness did not influence individual behavior in the central habitat (center angle ($t=0.14$, $p=0.89$), step length ($t=0.67$, $p=0.50$)).

Roesel's bush-cricket lives in moist tall-grass areas, identical to the habitat the central patch and the corridor consisted of. The short cut grass in the surrounding habitat represents an unsuitable matrix that would only be used when individuals are forced to move between patches of suitable habitat. In this study 40% of individuals remained in the central habitat. When the small size of the central patch is considered with the high movement activity and edge avoidance behavior of the bush-crickets within it, this demonstrates an unwillingness to leave the central patch across an edge despite an opportunity to do so. A reluctance to move out of patches is also reported in butterfly species (Schultz 1998), beetles (Bohlen & Barrett 1990) and bush-crickets (Kindvall 1999).

If the matrix did not affect individuals emigrating from the central patch, movement across it would be random. In the experiment it is expected this would be 85-90% of the dispersing individuals. However only 56% of the dispersers moved over the matrix, which is significantly less than expected. The individuals thus demonstrate an avoidance of the matrix, and the corridor proved to be a preferred alternative for dispersal. This behavior is recorded in both mammals (Davis-Born & Wolff 2000) and insects (Haddad 1999). The effect of matrices on individual movement behavior may differ for several reasons. Firstly, the matrix may consist of different biotopes with different structures. Secondly, different species may respond differently to the same matrix. Finally, different individuals (of the same species) may behave differently when put in same situation. In this study many individuals of the same species were confronted with the same situation (same type of matrix) and showed a difference in behavior after release.

The absence of effect from the type of edge was notable. An effect of edge softness (hard versus soft edges) has been discussed in an earlier paper (Stamps, et al. 1987). Advocates of soft edges argue that these serve as a buffer zone between habitats and matrix to facilitate movement between different habitats. Contrary to this I did not see any effect of edge type on dispersal behavior. Individuals did not move more often over matrix with soft edges. The avoidance of the matrix seems to be the dominant factor and is not influenced by the type of boundary. An alternative interpretation for this lack of effect is that adult male Roesel's bush-crickets do not perceive a difference between these two edge types. In their eyes, the edges may be equally soft or hard.

Whichever direction individuals moved when they left the central habitat, it was not predictable from the time of release to when they moved out from the center. This indicates that the decision process to leave does not differ between dispersal types.

Movement in corridors can be divided into three categories: 1) random walk, 2) density dependent movement, and 3) directional movements (Soulé & Gilpin 1991). In this study individuals moving through the corridor moved straighter than individuals that moved over matrix. This may be a result of the structure of the corridor steering movement in a more directed way (Tischendorf & Wissel 1997) (e.g. boundaries may guide individuals forward). Some studies suggest that movement velocity slows down in corridors (compared to habitat) because of the boundary effect of the corridor (e.g. increased mortality rate) (Soulé & Gilpin 1991, Tischendorf & Wissel 1997). As boundary encounters are determined by the corridor width, this would result in greater corridor width giving increased transition probability (Tischendorf & Wissel 1997). But others claim that there is an optimal width for a species (Soulé & Gilpin 1991, Andreassen, et al. 1996). A higher movement rate in matrix compared to corridors may be a result of an increased risk of predation, starvation or dehydration in the open habitat, which results in individuals moving more quickly towards the higher vegetation. Higher movement rates in matrix when compared with corridors have been noted in earlier studies (Andreassen et al. 1996, Schultz 1998). The size/width of the corridors in this experiment are not conducive to reproduction or feeding and thus are only used for dispersal. If they were suitable for reproduction and feeding it is expected that movement rates and behaviors in the corridors would be the same as for the central patch. This was not the case as individuals moved faster through the corridor when compared to their movement in the central patch.

When moving towards the edge individuals turning angles decreased and they moved back to the center. When they encountered the habitat edge they showed avoidance behavior, a reaction also reported in earlier studies (Mauremooto, et al. 1995, Davis-Born & Wolff 2000). It may be that this behavior is caused by an interest in investigating the area beyond the central habitat and an aversion to the open cut vegetation (Soulé & Gilpin 1991). The different edge types did not affect center angles or movement rates in the center. This lack of effect is probably due to the same reasons as discussed above.

Getting even - The effect of population and landscape variables on morphology and asymmetry

When populations are founded by small propagules there is a higher risk that they will have a lower genetic diversity than the population they originated from. Low genetic variability can show itself as reduced fitness of the individuals in the population. It can also result in a higher degree of asymmetry in morphological traits when individuals are exposed to stress from poor environmental conditions. To study the effect of different environmental and population variables on individuals' morphology I caught and measured individuals from a sample of the introduction sites (*Paper IV*). I found that long individuals were also heavier ($r=0.78$, $p<0.0001$). Individuals that were heavier had longer tibias ($r=0.72$, $p<0.0001$) and longer maxillary palps ($r=0.53$, $p<0.0001$). Longer individuals had also longer tibias ($r=0.55$, $p<0.0001$) and longer maxillary palps ($r=0.44$, $p<0.0001$). However, there was no correlation between the individual's weight or length and wing length.

There was no correlation of the degree of FA between the traits. Individuals' weight or length was not correlated with the asymmetry of the maxillary palps, tibias or wings. There was a correlation between length of the maxillary palps and its FA ($r=-0.14$, $p=0.040$), with longer palps being less asymmetric. Length of the tibia was not correlated with its asymmetry. There was a correlation between wing length and FA ($r=0.14$, $p=0.046$), in that individuals with longer wings were more asymmetric. The trait sizes or distribution or degree of asymmetry did not differ between individuals from the source population and individuals from the introduced populations.

There were differences between the sexes regarding every morphological character measured. Females were heavier ($\chi^2=79.87$, $p<0.0001$), longer ($\chi^2=78.0$, $p<0.0001$), had longer tibias ($\chi^2=62.31$, $p<0.0001$) and also longer maxillary palps ($\chi^2=55.52$, $p<0.0001$). The only trait found to be bigger in males was wing length ($\chi^2=61.97$, $p<0.0001$). There were no differences between the sexes in degree of FA in any of the three morphological variables.

Linear elements had different effects in males and females. In landscapes with more linear elements the females were shorter, but their tibias were longer. In these landscapes the males' tibias were also longer (Table 3). In most characters influenced, nodes had a positive effect. Females from populations with many nodes in the landscape were heavier but had shorter tibias, and males from those populations were longer, had longer tibias and wings (Table 3). Patch size had several positive effects on morphology. Females that came from populations with a large patch size were longer. Males that came from populations with large patch sizes had longer tibias and longer wings (Table 3).

The effect from initial size of the propagule differed. Males from larger propagules were longer and had longer wings, while females from those populations

Table 3. Summary of the forward, stepwise, linear multiple regression models identifying predictors of body weight, body length, maxillary palp length, tibia length and wing length in *M. roeseli*. For all populations mean values are used. Terms with more than one component, separated by x indicate interactions between component terms. The variables linear elements, nodes, patch size, propagule size, population growth, mean distance and all interactions between them were used in the test. Presented are only these that had a significant effect.

Variables	Estimate	F-ratio	d.f.	P
Dependent variable: Body length in Males				
Nodes	0.14	6.70	2	0.038
Propagule size	0.32	6.78	2	0.038
Mean distance	4.1×10^{-3}	31.55	1	0.002
Nodes x Propagule size	-68×10^{-3}	10.58	1	0.023
	N=159, R^2 Adj=0.840			
Dependent variable: Body weight in Females				
Nodes	-8×10^{-3}	84.17	2	0.002
Growth rate	0.58	120.03	1	0.002
Mean distance	-3×10^{-3}	77.09	2	0.003
Nodes x Mean distance	0.6×10^{-3}	145.26	1	0.001
	N=21, R^2 Adj=0.832			
Dependent variable: Body length in Females				
Linear elements	-0.13×10^{-3}	362.71	2	0.037
Patch size	17.09	8339.80	2	0.008
Growth rate	210.31	7974.90	2	0.008
Mean distance	-38×10^{-3}	163.27	2	0.055
Linear elements x Mean distance	2.7×10^{-6}	286.10	1	0.038
Patch size x Growth rate	-28.02	15943.00	1	0.005
	N=21, R^2 Adj=0.999			
Dependent variable: Tibia length in Males				
Linear elements	36×10^{-6}	83.50	1	0.003
Nodes	-0.79	50.59	2	0.005
Patch size	0.59	347.56	3	0.0003
Growth rate	10.70	161.50	2	0.0009
Nodes x Patch size	0.10	99.80	1	0.002
Patch size x Growth rate	-1.37	153.07	1	0.001
	N=138, R^2 Adj=0.994			

cont.

Variables	Estimate	F-ratio	d.f.	P
Dependent variable: Tibia length in Females				
Linear elements	0.2×10^{-3}	18.07	1	0.024
Nodes	-0.85	18.72	2	0.020
Propagule size	-0.45	17.64	2	0.022
Nodes x Propagule size	0.18	31.67	1	0.011
	N=20, R^2 Adj=0.829			
Dependent variable: Wing length in Males				
Nodes	0.70	96.01	2	0.0004
Patch size	0.97	82.57	1	0.0008
Propagule size	4.3×10^{-3}	63.38	2	0.0009
Growth rate	-1.67	18.87	1	0.012
Nodes x Propagule size	-0.13	53.98	1	0.002
	N=159, R^2 Adj=0.964			

had shorter tibias (Table 3). Growth rate had a positive effect on several of the morphological traits. In females a higher growth rate resulted in heavier and longer females, and males in populations with higher growth rates had longer tibias and wings (Table 3). The mean distance between individuals in the population affected females and males differently. When mean distance increased, males were longer while females were shorter and weighed less (Table 3).

There were several interaction effects (see table 3 for all). More significant than the variables alone were; nodes and propagule size on body length in males, nodes and distance on body weight in females, patch size and growth rate on body length in females, and nodes and propagule size on tibias in females.

For maxillary palps in males, linear elements and propagule size had a significant negative effect on FA, while patch size and growth rate had a significant positive effect. The interaction of linear elements and patch size was more significant than the variables alone (Table 4). In females, linear elements, nodes, propagule size and mean distance had significant positive effects on FA in maxillary palps. The interaction of propagule size and distance, and linear elements and nodes (both interactions more significant than the variables alone) were also significant (Table 4).

Table 4. Summary of the forward, stepwise, linear multiple regression models identifying predictors of fluctuating asymmetry (FA) in *M. roeseli*. Terms with more than one component, separated by x indicate interactions between component terms. The variables linear elements, nodes, patch size, propagule size, population growth, mean distance and all interactions between them were used in the test. Presented are only these that had a significant effect.

Variables	Estimate	F-ratio	d.f	P
Dependent variable: FA in Male Maxillary palps				
Linear elements	-0.23 x 10^{-3}	11.91	2	0.021
Patch size	-0.41	12.21	2	0.020
Propagule size	-0.04	14.57	1	0.019
Growth rate	0.87	98.70	1	0.0006
Linear elements x Patch size	32 x 10^{-6}	23.46	1	0.008
	N=159, R^2 Adj=0.945			
Dependent variable: FA in Female Maxillary palps				
Linear elements	-0.13 x 10^{-3}	498.47	2	0.032
Nodes	-0.90	518.15	2	0.031
Propagule size	-0.59	5138.60	2	0.010
Mean distance	-0.01	4663.80	2	0.010
Linear elements x Nodes	0.1 x 10^{-3}	908.91	1	0.021
Propagule size x Mean distance	0.01	9314.30	1	0.007
	N=21, R^2 Adj=0.999			
Dependent variable: FA in Male tibias				
Linear elements	38 x 10^{-6}	231.70	2	0.004
Patch size	0.02	18.80	2	0.050
Propagule size	0.15	301.30	4	0.003
Mean distance	-0.65 x 10^{-3}	685.49	2	0.002
Linear elements x Propagule size	-13 x 10^{-6}	292.55	1	0.003
Patch size x Propagule size	-5 x 10^{-3}	37.50	1	0.026
Propagule size x Mean distance	0.3 x 10^{-3}	175.07	1	0.006
	N=138, R^2 Adj=0.997			

cont.

Variables	Estimate	F-ratio	d.f	P
Dependent variable: FA in Wings in Males				
Nodes	0.10	123.11	3	0.008
Patch size	0.26	98.10	2	0.010
Propagule size	0.17	110.72	3	0.009
Mean distance	-2×10^{-3}	41.22	2	0.024
Nodes x Mean distance	0.4×10^{-3}	44.48	1	0.022
Nodes x Propagule size	-0.02	27.00	1	0.035
Patch size x Propagule size	-0.03	29.67	1	0.032
	N=159, R^2 Adj=0.981			

Tibial FA in males was negatively affected by linear elements, patch size, propagule size and mean distance (no interaction was more significant than the variables alone)(Table 4). In females, there was no effect of the variables on FA in tibias (Table 4).

In males, nodes had a significant positive effect, while patch size, propagule size and mean distance had a significant negative effect on FA in wings (no interaction was more significant than the variables alone)(Table 4). In females, no effect of the variables was found in FA of wings (Table 4).

Six years after introduction, variation in the average morphology of individuals in the different sized populations could be demonstrated. In males, a large propagule size increased the size of several traits. The opposite was seen in females. The impact of a small propagule size on males may be a founder effect resulting in smaller animals with shorter wings. Males from small propagule sizes were also more asymmetric than males from other populations, but this was not seen in females. The effect in males may be a result of a genetic diversity loss in the small populations resulting in a decreased opportunity for the males to cope with environmental stress and a reduced ability to allocate resources to the growth of their body and their stridulating organs. Nodes and propagule size together enhanced each other's positive effect on male body length so that males from large propagule sizes in landscapes with many nodes were longer than all other males. This might be an effect of the increased dispersal ability that nodes offer (Forman & Godron 1986, Berggren, et al. 2001), resulting in increased areas to reach for foraging and mating. The same interaction had a negative effect on female tibias.

A high population growth rate produced heavier and longer females. Males from populations with a high growth rate had longer tibias and longer wings. The fact that traits were smaller in slower growing populations might be an effect of genetic loss. Higher population growth rates are a reasonable indication that individuals are successfully reproducing and utilizing resources in the area. For female length, patch size and population growth rate enhanced each other's effect so females from large patch sizes that had high population growth were also longer. The high population growth rate did not decrease asymmetry in the populations.

It is interesting to note that a dense population (shorter distances between individuals) shows an increase in female length and weight but a decrease in male length. Populations with larger distances between individuals have to increase their efforts to find a mate. This additional energy expenditure may limit other necessary activities in the life of the animal (foraging, predator avoidance) and decrease the number of mates to choose from (Gilpin & Soulé 1986). The high degree of explanation in the interaction between nodes and distance in the effect on female weight indicates that females in populations with greater interconspecific distances benefited from an increased number of nodes in the landscape. The nodes may have been of greater importance for effective dispersal when there were long distances to cover between individuals. A sparser population may be beneficial for males, when it reduces both food and mate competition. This interpretation is likely as orthopteran males predominantly hold positions to stridulate to attract females, while the females move around to different males (Marshall & Haes 1988).

The positive effect of a large patch size on both male and female trait sizes might be because more food is available in larger habitat patches, enabling better body growth (Ehrlich & Murphy 1981). A large patch may also deter some individuals from emigrating (Kindvall 1995, Kuussaari et al. 1996), and thus preserve genetic material through increased available mate choice. The combination of an initially large habitat patch and a population with a high growth rate further increased body length in females.

Increases in the amount of linear elements and nodes increased the size of the traits in males. This may be a result of these landscape variables providing good resources for individual body growth. It may also be an effect of increasing habitat heterogeneity and thus increasing the possibility of finding food, both locally and regionally if conditions deteriorate (Kindvall 1996). This may affect individuals directly (survival), and also indirectly through an increased population size and a better chance of maintaining genetic diversity.

I found no correlation between the different trait asymmetry values, in contrast to some earlier studies (Lens & Van Dongen 1999), but supporting the findings in (Hunt & Allen 1998). A correlation of these traits would allow researchers to rely on a single measure as an accurate general assessment of asymmetry. My results suggest that to definitively assess asymmetry, several traits need to be measured, as differences in phenotypic development and susceptibility to environmental disturbances may be reflected in asymmetry in different morphological traits during different life stages. No correlation between fitness indicators as body weight and length and FA was found. Some earlier studies have shown this (Bennett & Hoffmann 1998, Uetz & Smith 1999), but others have not (Preziosi, et al. 1999).

FA of traits in males decreased with an increase in almost all variables. The variable that resulted in the lowest FA was propagule size, followed by linear elements and distance between individuals. This may be an effect of habitat availability and reduced environmental stress for the individuals and also that a population that is more genetically diverse is more resilient towards disturbing factors (Saccheri, et al. 1998). The FA of the different traits in females was not as significantly affected by the different variables as the male FA was. Less than 1/3 of the traits were affected by the variables and all of these were positive effects. An interaction between propagule size and distance increased the FA in maxillary palps and tibia in females. Why this effect should be seen when conditions are good is unclear.

There were significant differences between the sexes in the morphological traits measured. Females were bigger overall when compared to males, with the exception of the wings. As in many orthopteran species, *M. roeseli* males use their wings for stridulation to attract females. A well developed and long stridulation organ may increase the effectiveness of the call (Gwynne & Bailey 1988, Bennet-Clark 1998).

A general finding of this study showed that males were more affected by both landscape and population variables than females. Males seem to be able to utilize or allocate the increased amount of available habitat locally (patch size and linear elements) and regionally (linear elements and nodes) in producing a larger body. It is easy to assume that females rather than males have more to lose in terms of reproductive capacity when habitat is suboptimal or minimal. In orthopterans however, males put a huge effort into stridulation (Prestwich & Walker 1981). This is their main activity during the breeding season and they start to call in the morning as soon as they are warmed up and continue until the evening when the temperature cools. It has been noted that during long warm summer days, stridulation becomes erratic towards the end of the day (pers. obs). This is possibly a sign of exhaustion in the males. The nutritional requirements needed to support this high-energy activity must be quite large. Another explanation for the lack of increase in female trait size in good habitat is that they may allocate increased resources to egg production (i.e. more or bigger eggs), which was not examined in this study.

For females, high population growth and density (short distances between the individuals) appeared to be important. A rapid increase in population size also reduces the risk of losing genetic diversity (Nei, et al. 1975). Larger distances between individuals mean that a population is more widespread in the landscape. If the mean distance between individuals is small, the population is at a higher density and therefore has greater competition for resources. It also means that individuals have greater opportunities to find not only one but several mates. A response of females' size to lower density and low population growth may be an effect of genetic loss that cannot be compensated for by an increase in available habitat. Despite earlier findings that suggest the species does not have a problem in finding mates at low densities in a homogenous landscape (Kindvall et al. 1998), a heterogenous landscape (such as we studied here) might result in them having a reduced set of mates to choose from and copulate with.

This study indicates that particular environmental and population genetic variables were important in producing large individuals and decreasing FA. Even though this study was done in introduced populations, its findings could be applied to already established populations. In metapopulations, probability of successful establishment is supposed to increase with increasing number of individuals used in a introduction, increasing population growth rate, increasing migration rate and decreasing stochasticity (Hanski 1999). With few exceptions (see (Saccheri et al. 1998), it is not generally appreciated that even established small populations can be similarly affected by the variables examined in this study. This is especially likely considering repeated local extinctions and re-colonizations that continuously occur in metapopulations. This produces a similar effect to introductions with a decrease in genetic diversity from repeated founder effects occuring with small numbers of migrants (Gilpin 1991).

Another important conclusion to draw from this study is that differences between the sexes can be significant when studying the effect of different variables on both morphology and asymmetry. This means that results and predictions derived from data based on only one sex may be incorrect or misleading if generalized to the other sex or the population at large. The underlying reasons as to why the different sexes would respond differently to landscape or population characteristics are not always clear, and thus without empirical evidence it should not be assumed that results derived from one sex are representative of the whole population.

Conclusions

For the successful introduction of a population and an acceptable population growth rate, both the size of the introduced propagule and the quality of the landscape must be above a reasonably well defined minimum value. This is not only to maximize short term effects, but to secure a long term surviving population. This can be defined as a population with enough genetic diversity to withstand the stress that the environment and the population itself can inflict as a result of fluctuating conditions in and between seasons.

Understanding population dynamics in a modified landscape is the key to successful management of the world's species. This is true for species that are managed in 'naturally' occurring populations and those that are introduced into new areas. This study shows that the ability of animals to move between patches is a very important aspect for increasing the chances of a population surviving. The linear landscape elements and nodes are a vital structure in landscape management for a number of reasons. Firstly, they offer an increased area of suitable habitat for the species in question. Secondly, they facilitate movement between favorable habitat patches allowing successful expansion of the population with minimal loss of individuals in unfavorable matrix. Thirdly, high connectivity increases the possibility for interchange of individuals between populations and thus maximize genetic flow. And finally, nodes make it possible for individuals to re-direct their movements and offer an opportunity for faster dispersal over larger areas. It is my conclusion that for this species and probably for other similar species of Orthoptera, linear elements in form of corridors are preferred for dispersal. These corridors appear to have a positive influence on individuals dispersing through the landscape. This is desirable, both in agricultural and forested landscapes to reduce the negative effects of fragmentation on local population persistence. Corridors should now be seen as important tools in conservation for species where they enhance dispersal by encouraging individuals to move between habitats and increase their overall movement rate in fragmented areas. As linear elements are reduced by human modification of the landscape (Ruuska & Helenius 1996), more consideration should be taken in preserving those that remain. In addition, creation of new linear elements may be beneficial for a majority of species (Weaver, et al. 1996, Sternberg 1998, Collinge 2000) especially in acutely fragmented landscapes.

If we consider being big and symmetric as good things to be (Bennett & Hoffmann 1998, Thornhill & Møller 1998), and markers of good condition, understanding what influences these attributes in individuals will be valuable in species conservation. This study shows that both environment and population genetics were important to produce large individuals and decrease FA. Despite the study being undertaken in introduced populations, the results should be seen as being more generally applicable to already established populations also.

Taken together, these studies increase the knowledge of how introduced populations are affected by both the landscape they are introduced into and the inherent properties of the population. I have shown that it is possible to estimate the number of individuals needed to successfully establish a growing population. Also it can be seen that the total area of different habitats and the connectivity between these are important for colonization success, growth rate and dispersal. The importance of linear elements in the landscape and the connection between these are of special importance. Finally, the landscape, the propagule sizes, their growth rates and the population's dispersion can all affect the evolutionary development of the population.

Many insect species are threatened today, and among them several orthopteran species (Marshall & Haes 1988, Cherill & Brown 1990, Fry & Lonsdale 1991, Meads 1995, Haes & Harding 1997, Gärdenfors 2000). In Sweden, the bush-cricket *Metrioptera bicolor* is considered vulnerable (Gärdenfors 2000). The main reason being reforestation leading to fragmentation of its former distribution area, leaving only 13% of the suitable habitat intact (Kindvall 1993).

I have shown in these studies that it is possible to use a species as a model organism to study what affects the success and fate of introduced populations. It is possible to study these effects in the species' natural environment. There remains the question of whether the results from this study can be transferred to similar species or to conservation in general. I believe these results are valuable for conservation biology as they indicate the types of information that may be important for population management. For similar species living in similar habitats with a comparable life history I would use these results to pinpoint important variables affecting conservation work with the target species. These results give good clues as where to best focus conservation efforts, both if additional research in the target species is required, or how the introduction would be planned if there were no possibility to undertake specific research in the target species.

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The department has been like a second home to me all these years. This is due to all the lovely people that work there, that are deeply devoted to their jobs. From the first day that I sat my foot in the house I have felt welcomed and that is one of the best feelings you can have in a workplace. An excellent fellow PhD student has

Staffan Roos been, except from being a very good friend and a social model, he always has good ideas and lends a hand when help is needed. An extra plus for sending stupid things he finds on the net and answering me when I shout across rooms (not going the few steps to his room). Bosse Söderström started as a PhD-student about the same time as I. He has always been a researcher model with his accuracy and professionalism. He has also been a good friend for a long time and keeps inspiring me with his fearlessness in challenging new projects. Jonas Welander has for a long time been a fellow PhD-student to discuss work and non-work things with and he has never backed down to help fixing parties, barbecues or other activities. He has also entertained me with his funky ideas (mostly in the technical area) and his long term projects (clue = renovate). He and Staffan have also letting me ride in to town with them zillion times (when their cars were comfortable and quick compared to my bike). The younger bunch (Ermias Azeria, Anders Glimskär, Anders Jarnemo, Per Johansson, Bosse Söderström, Staffan Roos, Johan Samuelsson, Henrik Weibull, Jonas Welander, and Johan Åberg) as we see ourselves, have had lots of good times together. Just making short (or long) visits in each others offices to help or give an opinion on something or just for plain gossip. One thing as valuable as the other. There has always been a good spirit among us and outside work, there have also been good evenings at the pub or shooting pool. Thank you youngsters, keep the tournaments rolling! I also want to thank Martin Tjernberg for the lovely bush-cricket drawings and Torbjörn Persson for always being there to help when the computer doesn't do what it is supposed to do.

I want to thank all the staff at CBM for giving me something else than my research to think about when working with them. Special thanks to Mats Höggren (with good older brother qualities) and Thomas Elmqvist for being training buddies when the spirits moved us.

It is also a life outside the department. Even if it doesn't feel like that all the time. But family and friends (other than those at the department) make the rest of my time a very good one. My mum Gunilla and my dad Gunnar have always supported me in my decisions in life (at least when I got a bit older). With joyous acclamations they have followed my career and have been sad with me when things were tough, and happy with me when things worked fine. They have also supported me financially many times especially in the beginning as a PhD-student when I had no salary. For all their support and help I owe them a immensely and they have my deepest thanks. My brother Björn always lifts my spirit with his great sense of humour and all his adventures. He shows me that live can also involve other things than work - like play. He has also helped many times with field work, when I was over my head. Thank you, you are the best brother!

I have several friends that bring me joy. During my research preparation course (zooekologi) I met Anna Karlsson and Anna Lindvall. We ended up as PhDstudents in different departments, working with totally different things but experiencing many similar things. They have during this time been a very good support as friends and have shown me in different ways that life can be more than research. Sometimes they remind me of what I said as a last year student "I will never work with birds or bugs because they were boring". I ended up doing my exam work with birds and then spend my PhD-with this bug. One can say that I wasn't really right that time. Other important friends have Christina Wikman and Lena Alfvén been. Thank you for an easygoing, unreserved friendship. My cousin Elisabeth Jansson is not just a cousin, she has also been a good friend. Big thanks also to Kattis Sandberg for many fun days, you are like my sister.

Thank you Tommy for being a reason to do other things than work and never complaining when work took a lot of time from other activities. Matt you have given me energy to work and get things rolling, and for all stand by help that you have given - I am deeply grateful. Go royal marsupials!

And last but not least – thank you all bush-crickets that have helped me so kindly over the years. Without you, nothing of this would have happened. Keep on jumping. Conquer new grounds. These years have been some of the best of my life and it is with a bit of sadness that I now have reached this goal and have finished – for now. I am going from one instar to another (I'm pretty sure I'm not an adult yet) and I am curious of the future and grateful of the past.